Campylopus introflexus invasion in a dune grassland: Succession, disturbance and relevance of existing plant invader concepts

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Abstract: HASSE, T. 2007. *Campylopus introflexus* invasion in a dune grassland: Succession, disturbance and relevance of existing plant invader concepts. – Herzogia **20**: 305–315.

The impact of the exotic moss *Campylopus introflexus* on acidic, nutrient-poor sand grassland vegetation in the central Netherlands was assessed. Eighteen permanent plots, distributed among three different treatments, were studied during five years: stands with massive invasion of *Campylopus*; stands with sparse occurrence of *Campylopus*, dominated by the native moss *Polytrichum piliferum*; and experimentally disturbed *Campylopus*-invaded stands. Frequencies of all species present were recorded and trends were analysed graphically as well as statistically using Redundancy Analysis (RDA) for repeated measurements.

In all three treatments, the often-described succession of acidic dune vegetation from moss-dominated to lichen-dominated stands was demonstrated by a slow accumulation of lichens. Neither the dominance of *C. introflexus* nor the experimental disturbance of the moss carpets into fragments had major impact on the vegetation succession. The results suggest that when sufficient adjacent sources of lichen diaspores are available, lichens tend to re-colonize the moss carpets. Consequently, under such conditions, the *Campylopus*-invasion seems to have only a temporary impact in a certain successional phase.

This study shows that general plant invader hypotheses for exotic vascular plants are only partly appropriate for *C. introflexus*. The existing concepts for plant invasions therefore have to be amended to allow their application to bryophytes.

Zusammenfassung: HASSE, T. 2007. Invasion von *Campylopus introflexus* in einem Dünengrasland: Sukzession, Störung und Bedeutung bestehender Hypothesen für invasive Pflanzenarten. – Herzogia **20**: 305–315.

Die vorliegende Untersuchung befasst sich mit dem Einfluss des neophytischen Mooses *Campylopus introflexus* auf saure, nährstoffarme Graslandvegetation. Während fünf Jahren wurden 18 Dauerbeobachtungsflächen in den zentralen Niederlanden untersucht, die jede einer von drei verschiedenen Behandlungen zugeordnet wurde: 1. von *Campylopus* dominierte und vollständig überwucherte Bestände, 2. von *Campylopus* spärlich besiedelte, von *Polytrichum piliferum* dominierte Bestände, 3. von *Campylopus* überwucherte Bestände mit experimenteller Störung. Frequenzen aller vorkommenden Arten wurden erhoben und Trends wurden grafisch analysiert sowie statistisch mittels Redundanzanalyse (RDA) für Messwiederholungen.

In allen drei Behandlungen deutete eine langsame Anreicherung von Flechten auf die vielfach beschriebene Sukzession von Moos-dominierter zu Flechten-dominierter Dünen-Vegetation hin. Weder die Dominanz von *C. introflexus* noch die experimentelle Fragmentierung der Moosteppiche hatten einen Einfluss auf die Sukzessionsentwicklung. Die Ergebnisse zeigen, dass unter Vorhandensein von ausreichend Erdflechtendiasporen, wie dies im Untersuchungsgebiet der Fall ist, die Moosteppiche von Flechten besiedelt werden. Unter diesen Bedingungen scheint die *Campylopus*-Invasion nur vorübergehende Auswirkungen in einem bestimmen Sukzessionsstadium zu haben.

Die Untersuchung zeigt, dass Hypothesen, die unter Betrachtung von neophytischen Gefäßpflanzen erarbeitet wurden, sich nur bedingt auf das Verhalten von *C. introflexus* anwenden lassen. Bestehende Invasions-Konzepte müssen demzufolge erweitert werden, um auch für Moose Anwendung finden zu können.

Keywords: Bryophytes, *Corynephorus canescens*, Gray Hairgrass, Heath Star Moss, impact, lichens, neobiota, Netherlands.

Introduction

The Heath Star Moss (*Campylopus introflexus*) is an invasive, exotic moss species in Europe and North America. The moss originates from the southern hemisphere where it is known from southern South America, South Africa, southern Australasia and several islands in the southern oceans (HASSEL & SÖDERSTRÖM 2005). However, it is unknown from which continent the species invaded Europe and North America (STECH & WAGNER 2005). It was first reported from Europe in 1941 (from Great Britain: RICHARDS 1963) and from North America in 1975 (FRAHM 1980). *Campylopus introflexus* spread quickly from the most oceanic temperate to more suboceanic or even subcontinental regions. Today, in Europe it is known from Portugal to Iceland, Norway and Sweden in the North as well as from Lithuania, Poland and Italy in the East. In many European countries, the species is reported to be invasive (e.g. Netherlands: VAN DER MEULEN et al. 1987, Great Britain: EQUIHUA & USHER 1993, Germany: BIERMANN & DANIELS 1995, Belgium: STIEPERAERE & JACQUES 1995, Portugal: SÉRGIO et al. 2003).

The species prefers dry to wet open sites with leached, acidic (pH 4–6), nutrient-poor sandy soils, and only sparse herb vegetation. These habitats are found on inland dunes, acidic coastal dunes, on bog soils and in wet heaths. Furthermore, it occupies clay, rotten wood and tree bases. Sites are often associated with human or natural disturbances such as burning or cutting of sods, digging by rabbits, erosion by wind and rain water, game trampling or geothermic activities (VAN DER MEULEN et al. 1987, EQUIHUA & USHER 1993, BIERMANN 1999, VILMUNDARDÓTTIR et al. 2006, pers. observ.).

The species has a high reproductive output by producing both sexual and asexual diaspores. The latter are represented by shoot fragments, which easily break off and are blown away by wind. Additionally, larger fragments of carpets can be dispersed by different disturbance agents and stay alive several years (VAN DER MEULEN et al. 1987) to re-establish once suitable conditions arise (EQUIHUA 1991).

Campylopus introflexus can form extensive dense carpets of high dominance and is suspected to have an impact on habitat conditions and the native flora. POTT (1995) even used the term 'shroud' („Leichentuch") in this context, indicating that the moss carpets permanently displace the native vegetation. Carpets of the moss can reach 2–10 cm thickness and strongly alter habitat conditions: they cover mineral substrate and decrease the water supply for other plants by interception, both resulting in impaired conditions for germination (cf. BECHTEL et al. 1998, BIERMANN & DANIËLS 2001, BÖGER 2002).

Crevices in the aged moss carpets, created by periodical drying as well as disturbances such as trampling by game or digging by rodents and, most importantly, by birds in search for insects, frequently lead to the massive segmentation of these carpets into numerous fragments of a few centimetres in size. The impact of this fragmentation on the succession has not been studied so far.

In the *Corynephorus canescens* grassland on acidic dunes in the central Netherlands, *Campylopus introflexus* colonizes niches similar to those of the common native moss species *Polytrichum piliferum*. Both species colonize stabilised, bare, sandy soils and gaps between higher plants, *C. introflexus* being more successful in the latter (HASSE 2005, HASSE & DANIËLS 2006). After disturbance events these gaps can also occur amidst lichen carpets leading to the observation that the moss can also replace lichen vegetation. Considering these gaps as sites of regressive succession, one can assert that both species establish in an early to intermediate successional phase in *Corynephorus*-dominated grassland.

The impact on the short-term vegetation succession in dry dune grassland has not been examined to date. A comparison of the succession of co-occurring species in stands dominated by either *P. piliferum* or *C. introflexus* is undertaken in order to analyse the impact of the exotic moss in *Corynephorus canescens* grassland. Special attention is paid to the lichens, which are often observed to replace pioneer mosses during succession in this kind of vegetation (e.g. BIERMANN 1999). The mechanisms behind this moss-to-lichen succession have previously not been investigated for the invasive *C. introflexus*.

In this five-year experiment, the following specific questions were addressed:

(1) Does *C. introflexus* invasion alter the succession of *Corynephorus* vegetation?
(2) Does the frequently occurring fragmentation of the moss carpets influence succession?
(3) Does the performance of *C. introflexus* fit into general concepts for plant invaders?

Methods

Experimental design

Field work was carried out in an extensive inland dune area in the National Park 'De Hoge Veluwe' in the central Netherlands (52°04'27"N/5°51'29"E). This area is characterized by oceanic climate and acidic, nutrient-poor and poorly developed sandy soils on drift sand. The low dunes are predominantly covered by *Corynephorus canescens* grasslands as well as by *Festuca filiformis* grassland, *Calluna vulgaris* heath and *Pinus sylvestris* forest (MASSELINK 1994, HASSE et al. 2002).

Surveys took place in each year from 2002 to 2006 in spring to early summer. For each of the following three treatments, six permanent plots (0.3 m × 0.3 m) were established: (1) stands massively invaded and dominated by the exotic invader *C. introflexus*; (2) stands with dominance of the native *P. piliferum* and with sparse occurrences of *C. introflexus*; and (3) experimentally disturbed stands dominated by *C. introflexus*. In massively invaded stands (1 and 3), the cover of *C. introflexus* was nearly 100 % whereas in stands with treatment 2, it was only 5–15 % despite high frequency values. The term 'massively invaded' therefore refers to situations in which the invading species was not only present but also reached high cover values, thus contributing substantially to the structure of the vegetation stand. One plot of treatment 1 was destroyed during the first observation year and therefore the data discarded, leaving n = 5 replicates. The plots were randomly distributed in areas of approximately 0.5 hectares (*P. piliferum*) or 1.0 hectares (*C. introflexus*) respectively. A minimum of three meters distance was kept between the plots.

The object of the comparison between treatment 1 and treatment 2 was to address whether massive *C. introflexus* invasion alters the succession of *Corynephorus* vegetation (1). Both treatments were regarded as similar successional phases where one was successfully and massively invaded by the exotic moss and the other was not. Differences in the succession of the two treatments were interpreted as the effect of the exotic moss invasion.

Comparing treatment 3 with treatment 1 was intended to address whether the frequently occurring fragmentation of the *C. introflexus* carpets influences succession (2): Disturbance was carried out once after the first survey in 2002 by segmenting the moss carpets together with their co-occurring species into fragments of 5 cm × 5 cm size and rearranging them chaotically in the plot, thus simulating the frequently observed disturbance by animals (Fig. 1).

The relevance of general plant invader hypotheses for the performance of *C. introflexus* was assessed by evaluating all results and including additional observations as well as findings by other authors.

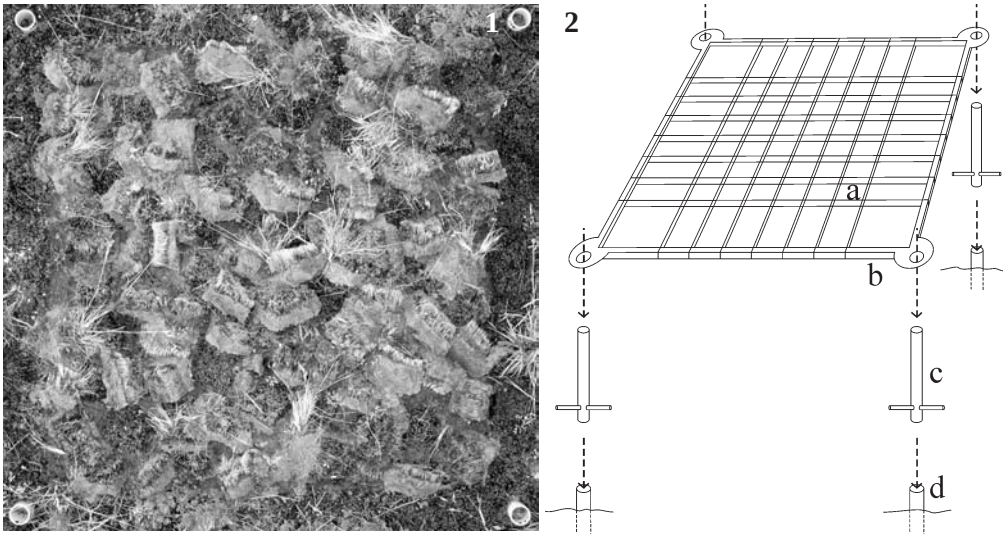

Fig. 1: Disturbance treatment applied to *Campylopus introflexus* stands in 2002 after the first data recording.
Fig. 2: Tools for recording of species frequencies in a permanent plot. a) A nylon thread forms two congruent grids of 6 × 6 square cells (each cell 5 cm wide) set up one above the other. It is mounted on b) an aluminium frame which for recording was put on c) four wooden sticks which exactly fit into d) the four plastic tubes permanently placed into the soil.

For data recording, each permanent plot was subdivided into a grid of 6 × 6 cells of 25 cm² each (Fig. 2). The deviation of the measurement position from year to year was estimated to be < 2 mm. Presence/absence for each species in each cell was recorded and subsumed into species frequency (1–36) per plot. Species cover values were also taken into account in a more complex analysis. They led essentially to the same results and are therefore presented here only for descriptive purpose in Fig. 3. Primary thalli of *Cladonia* species consisting of squamules were identified to species level if belonging to '*C. cervicornis* + *C. verticillata*', *C. coccifera* (*C. diversa* sensu STENROOS [1989]), *C. borealis* or *C. strepsilis*, and were otherwise aggregated to '*Cladonia* squamules'. Poorly developed specimen which could not be identified in the field were sampled by small thallus fragments and identified by use of thin-layer chromatography (ORANGE et al. 2001) or UV-fluorescence in the laboratory. Nomenclature follows WISSKIRCHEN & HAEUPLER (1998) for vascular plants, KOPERSKI et al. (2000) for bryophytes and VAN HERK & APTROOT (2004) for lichens.

Data analysis

To visualise the changes, mean frequencies of selected species were plotted against the year for each of the three treatments.

Differences in the vegetation succession of treatment 2 against treatment 1, and of treatment 3 against treatment 1 were tested separately. The tests were performed once including all taxa except *P. piliferum* and *C. introflexus*, and once including only lichens. The frequency values of the two mosses, *P. piliferum* and *C. introflexus*, were not taken into account, since their different abundances represent the two different treatments of *Campylopus*-invasion and no invasion. The changes of the mean species frequencies were compared for the whole period

2002–2006 as well as only for the first year (2002–2003) in which the disturbance treatment was carried out.

For the eight different tests (Table 2), Redundancy Analyses (RDA) with Monte Carlo permutation test in the CANOCO package were used (TER BRAAK & ŠMILAUER 2002). This approach is similar to that used by LEPŠ (1999). The differences in vegetation trends between the treatments were tested for significance by using the appropriate combinations of explanatory variables and covariables in RDA, together with the appropriate permutation scheme in the Monte Carlo test. In this case, explanatory variables were defined as year × 'treatment 2' or year × 'treatment 3' respectively, thus corresponding to the 'effect' of the *P. piliferum*-dominance (2) or experimental disturbance (3) in comparison to undisturbed *C. introflexus*-dominance (1). The plots were coded as binary variables (dummy variables) and used together with the year as covariables for each test. Consequently, the average over years of each plot is subtracted, and thus changes in each particular plot were analysed. Year was coded as linear parameter with –2, –1, 0, +1 and +2 for the years 2002 to 2006. Species scores on the constrained axis of analysis, where 'treatment 2' (or 3) × time is the explanatory variable, were considered characteristic of the species responses to the different treatment compared to treatment 1 (control).

Results

Baseline conditions in 2002 (Table 1) indicated that the moss carpets had already started to be colonized by lichens to a varying extent. Most successful were the species *Cladonia coccifera*, *C. ramulosa* and *C. floerkeana*. The latter two also contributed most to the 'artificial taxon' *Cladonia* squamules. Most lichens managed to colonize dead as well as living parts of the moss carpets. Despite the dominance of *P. piliferum* in treatment 2, the exotic *C. introflexus* was present with equal frequency due to small but numerous shoots growing amid the carpet of the native moss.

Overall, most species trends followed similar patterns during the experimental period across the three treatments (Fig. 3). Vascular plants showed similar fluctuations in all three treatments. The dominant grass *Corynephorus canescens* declined in the first two years due to unfavourable periods of droughts (HASSE & DANIËLS 2006) and additionally due to disturbance in treatment 3. The winter annual *Spergula morisonii* showed the same trend in the first year but was able to gain strongly in later years. Grass seedlings showed increased germination in the last year, but these mean frequency values were based on extraordinary dominances in one or two single plots. Lichens showed a gradual increase in all three treatments, except for the first year in the disturbed plots. However, these decreases were compensated partly in subsequent years. *Polytrichum piliferum* showed a steady frequency decline in the *C. introflexus*-dominated plots, whereas *C. introflexus* did not in the *P. piliferum*-dominated plots.

No differences in the vegetation development between undisturbed stands dominated by *P. piliferum* and by *C. introflexus* were detected (Table 2). However, the impact of the disturbance treatment in the first year on all plants and on lichen colonization in particular was affirmed by the permutation test. No effect of disturbance on the species succession was revealed for the total period of observation, even though the fragmentation of the moss carpet was still evident in the field in 2006. During the experimental period parts of the *C. introflexus* carpet fragments died off, but greater parts stayed alive. In some places the moss formed new shoots, apparently originating from stems or rhizoids.

Table 1: Baseline frequencies [1–36] per plot of all occurring species in 2002 among the three different treatments.

Treatment	1: *Campylopus*-dominance					2: *Polytrichum*-dominance						3: *Campylopus*-dominance, disturbed					
Replicate	1	2	3	4	5	1	2	3	4	5	6	1	2	3	4	5	6
Plot-no	151	153	154	159	160	61	63	66	76	78	81	152	155	156	157	158	161
Vascular plants:																	
Corynephorus canescens	31	23	28	33	2	.	5	10	10	17	23	25	29	18	5	28	23
Festuca filiformis	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.
grass seedling	2	5	1	.	2	.	3	2	.	5	2	1	4	.	.	.	.
Spergula morisonii	5	6	1	3	1	.	23	.	.	1	5	.	10	4	8	3	4
Mosses:																	
Polytrichum piliferum	18	23	28	17	34	36	36	36	36	36	36	6	11	20	25	33	4
Campylopus introflexus	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36
Lichens:																	
Stereocaulon condensatum	1	.	.	1	.	.	.	.	2	.	.	.	.	.	.	.	.
Cladonia cervicornis + *C. verticillata*	3	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.
Cladonia coccifera	11	10	4	11	33	.	29	3	15	4	15	10	9	9	21	19	25
Cladonia borealis	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Cladonia ramulosa	1	1	2	.	18	.	4	.	.	.	1	.	.	12	10	3	6
Cladonia glauca	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Cladonia floerkeana	1	2	.	2	1	1	3	3	1	.	.	3	2	3	3	8	3
Cladonia crispata	1	2	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.
Cladonia gracilis	.	.	.	.	.	.	.	.	1	.	.	1	.	1	2	.	.
Cladonia zopfii	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Cladonia uncialis	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Cladonia arbuscula	1	.	1	.	.	.	.	.	.	.	.	1	.	.	.	1	.
Cladonia squamules	.	.	2	2	6	.	1	3	.	.	4	2	1	2	1	6	2
Cetraria aculeata	.	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.

Carex arenaria, *Pinus sylvestris* seedlings, *Micarea denigrata*, *Placynthiella icmalea*, *Cladonia grayi* and *C. strepsilis* occurred during the subsequent years.

Table 2: Test for the 'effect' of *P. piliferum*-dominance (2) or experimental disturbance (3) in comparison to undisturbed *C. introflexus*-dominance (1) including different taxa and time periods. Results of the Redundancy Analysis (RDA) of species frequencies with Monte Carlo permutation test are presented. % expl. axis 1 = explanation of the species variance by the first ordination axis. *r* axis 1 = species-environment-correlation of axis 1. *F* = F-ratio statistic for the test on the trace. *p* = probability value obtained by the Monte Carlo permutation test (999 permutations) i.e. type I error probability in testing the hypothesis that the effect of the explanatory variables ('year × treatment 2' or 'year × treatment 3' respectively) is zero. Significant test results ($p < 0.05$) are indicated in bold.

Test: treatment (x) differs from (y)	Included taxa	Included time period	% expl. axis 1	*r* axis 1	*F* ratio	*p*
(2) from (1)	all except *P. piliferum* and *C. introflexus*	2002–2003	4.2 %	0.569	0.398	0.821
		2002–2006	9.3 %	0.562	4.290	0.053
	only lichens	2002–2003	9.5 %	0.678	0.943	0.395
		2002–2006	13.1 %	0.608	6.334	0.090
(3) from (1)	all except *P. piliferum* and *C. introflexus*	2002–2003	31.8 %	0.842	4.189	**0.005**
		2002–2006	4.5 %	0.370	1.966	0.090
	only lichens	2002–2003	38.6 %	0.771	5.647	**0.012**
		2002–2006	5.5 %	0.399	2.447	0.339

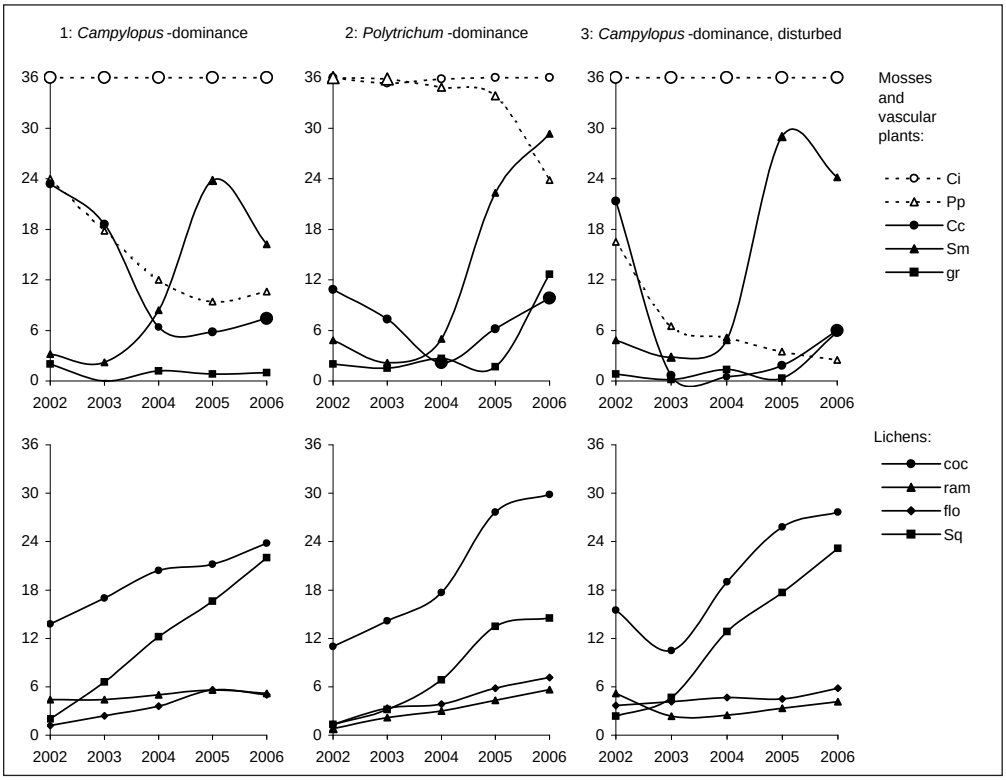

Fig. 3: Mean frequencies [1–36] of selected species in all plots separated by the three different treatments 1–3; Ci = *Campylopus introflexus*, Pp = *Polytrichum piliferum*, Cc = *Corynephorus canescens*, Sm = *Spergula morisonii*, gr = grass seedlings (mainly of *C. canescens*), coc = *Cladonia coccifera*, ram = *Cladonia ramulosa*, flo = *Cladonia floerkeana*, Sq = *Cladonia* squamules (see experimental design). Different medians of cover values per 25 cm² cell are represented by different symbol size: small: < 4 %, medium: 4–40 %, large: > 40 %.

Discussion

Succession and disturbance

Species stands dominated by the invasive exotic moss *C. introflexus* developed very similarly to stands of the native moss *P. piliferum*. Carpets of both species were gradually colonized by lichens, which may indicate that they are replaced by lichen vegetation in the long-term. Furthermore, there was no difference in the speed of this succession during the experimental period. Although it can be observed that *C. introflexus* replaces *P. piliferum* in large areas and thus alters ecosystem structure and function, its invasion seems to be limited to a particular successional phase. The data provide no evidence that it causes permanent damage to the development of *Corynephorus canescens* vegetation during a period of several years. This might be a consequence of the condition that the whole range of successional phases existed nearby, thus providing sufficient sources of lichen diaspores to re-colonize the moss carpets. Also MINARSKI & DANIËLS (2006) observed on a 936 m² plot that, after approximately 10 years of *Campylopus*-dominance in *Corynephorus canescens* grassland, the lichen vegetation conspicuously recovered during progressive succession. However, the relative decline of *P. piliferum* in comparison to *C. introflexus* in this study indicates a higher competitive capacity of

the non-indigenous moss species and shows that the latter is able to suppress the native moss. The strong decline of *P. piliferum* in treatment 2, though, could to a high degree be attributed to a gradual die-back after a severe drought in 2003 (HASSE & DANIËLS 2006). In situations where lichen diaspores are not available, for instance, if *Campylopus* has become dominant on the whole dune complex at the same time, a potential major threat by *C. introflexus* invasion to the native vegetation is conceivable.

The frequently observed disturbances of the moss carpets did not influence succession at the scale of five years. The loss in species abundances resulting from disturbance in the first year was compensated within one or two years. Hence, a single disturbance event did not change the direction of succession. Frequent major disturbances, however, might prevent the slow-growing lichens from successfully colonizing the moss carpets. Since the moss fragments mostly stayed alive and were able to form new shoots that colonized newly-created gaps, the dominance of the moss was not inhibited by these disturbances. Three years after the disturbance the first new continuous moss carpets started to form in the experimental gaps. Therefore *C. introflexus* can be characterized as being highly resistant to mechanical disturbance. Consequently, time and not disturbance leads to a replacement of these moss carpets by lichen vegetation.

The relevance of plant invader hypotheses for the performance of *C. introflexus*

Hypotheses and generalisations about plant invaders and invasibility of ecosystems (e.g. LONDSDALE 1999, DAVIS et al. 2000, THOMPSON et al. 2001, HERBEN et al. 2004, HIERRO et al. 2005 and LEISHMAN & THOMSON 2005) are mostly formulated on the basis of data from vascular plants. The question is: how far are these applicable to *C. introflexus* as an example of a moss invader?

According to recent interpretations of the species richness hypothesis (ELTON 1958, MACARTHUR 1970) for example by LONDSDALE (1999), species-poor communities are generally less prone to invasion, measured by the number of invading exotic species, than are species-rich ones due to their poorer habitat diversity. In acidic, oceanic, oligotrophic dune grassland, which is considered as species-poor (but moderately rich in terricolous lichen species), the moss *C. introflexus* is often the only exotic invader, which agrees with LONDSDALE (1999). Due to its effective clonal propagation, it is able to reach a cover of almost 100 % over large areas. Hence, adding more weight to the dominance of invaders than to their species number, the invasibility of the species poor *Corynephorus* grassland must be regarded as high.

DAVIS et al. (2000) and THOMPSON et al. (2001) suggested that infertile soils with low pH reduce the abundance of invaders. *Campylopus introflexus*, on the contrary, favours acidic nutrient-poor soils and is absent or less successful on calcareous sand and on more fertile ground where it is seemingly outcompeted by vascular plants.

The success of invasive species in a low fertility vegetation community is claimed to be facilitated by the addition of nutrients (LEISHMAN & THOMSON 2005). This was also assumed for *C. introflexus* in *Corynephorus* vegetation by KETNER-OOSTRA & SÝKOYA (2000). However, no significant effect of increased nitrogen input on *C. introflexus* invasion was revealed in field experiments (HASSE & DANIËLS 2006).

A plant community should become more susceptible to invasion whenever the amount of unused resources increases (DAVIS et al. 2000, THOMPSON et al. 2001). In the case of *C. introflexus*, such an unused resource is first of all space, which is made available through disturbance and

through which light and rain water are more freely accessible. Soil water and nutrients are barely relevant since mosses gather nutrients basically from air-borne depositions or possibly by recycling dead material (VAN DER MEULEN et al. 1987). Light is not a limiting resource in the open dune habitats.

The empty niche hypothesis (ELTON 1958, MACARTHUR 1970, HIERRO et al. 2005), postulating that exotics utilise resources unused by natives, is only partly appropriate for *C. introflexus*. The native *P. piliferum* is a direct competitor of the invader in colonizing gaps, although the niches are not completely congruent. *Polytrichum piliferum* spreads below-ground via rhizoids and therefore has advantages on moving sands, whereas *C. introflexus* predominantly propagates above-ground via shoot fragments, preferably on settled sands that are enriched with some litter or humus (BIERMANN & DANIËLS 1997, HASSE & DANIËLS 2006). The decline of sand drift dynamics in the last decades may have promoted the spread of *C. introflexus*, since it has been observed that sand drift inhibits the expansion of *C. introflexus* (VAN DER MEULEN et al. 1987, VAN BOXEL et al. 1997, KETNER-OOSTRA & SÝKORA 2000).

The disturbance hypothesis (BAKER 1974) finally suggests that exotic species are adapted to disturbances that are novel to natives. This hypothesis is not applicable here. *Campylopus introflexus* indeed benefits from gaps created by small-scale disturbance that it exploits more rapidly than the native species, and it has been observed repeatedly that disturbance promotes the invasion of *C. introflexus* (e.g. VAN DER MEULEN et al. 1987, EQUIHUA & USHER 1993, BIERMANN & DANIËLS 2001). The grassland vegetation on dunes, however, is an initial phase of their succession, and depends on disturbance. The native species are therefore as well adapted to disturbance.

Consequently, the expansion of the terricolous moss *C. introflexus* follows to some degree the patterns formulated in hypotheses for vascular plant species, but there are also distinct deviations as outlined above. The existing concepts therefore need to be amended to allow their application to bryophytes.

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